THE ROYAL SOCIETY

Visual specialization and brain evolution in primates

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Several theories have been proposed to explain the evolution of species differences in brain size, but no concensus has emerged. One unresolved question is whether brain size differences are a result of neural specializations or of biological constraints affecting the whole brain. Here I show that, among primates, brain size variation is associated with visual specialization. Primates with large brains for their body size have relatively expanded visual brain areas, including the primary visual cortex and lateral geniculate nucleus. Within the visual system, it is, in particular, one functionally specialized pathway upon which selection has acted: evolutionary changes in the number of neurons in parvocellular, but not magnocellular, layers of the lateral geniculate nucleus are correlated with changes in both brain size and ecological variables (diet and social group size). Given the known functions of the parvocellular pathway, these results suggest that the relatively large brains of frugivorous species are products of selection on the ability to perceive and select fruits using specific visual cues such as colour. The separate correlation between group size and visual brain evolution, on the other hand, may indicate the visual basis of social information processing in the primate brain.

Keywords: brain size; primates; vision; parvocellular; frugivory; social cognition

1. INTRODUCTION

Primates have large brains. They also have several distinctive features of the visual system, including frontally directed eyes, a distinctly layered lateral geniculate nucleus, a high degree of binocular integration, and high visual acuity (Allman & McGuinness 1988). These features are accompanied by a complex arrangement of highly interconnected and numerous cortical visual areas: in macaques there are 305 known pathways connecting 32 cortical visual areas. Visual areas make up about 50% of the entire neocortex (van Essen *et al*. 1992; Drury *et al*. 1996). In the light of these facts, it is perhaps surprising that theories of brain size have until now largely ignored the possible role of visual specialization. Here I test the hypothesis that brain size is associated with visual specialization using comparative data on the size of relevant brain structures.

A feature of primate visual specialization is the existence of two physiologically distinct pathways. The parvocellular system primarily analyses fine detail and colour, whereas the magnocellular system is primarily involved in movement detection and the analysis of dynamic form (Livingstone & Hubel 1988; Zeki & Shipp 1988; Allman & McGuinness 1988). This anatomical and functional segregation originates prior to cortical processing, with distinct parvocellular and magnocellular layers present in the lateral geniculate nucleus (LGN), which projects to the primary visual area of the cortex (striate cortex, or V1), and thence to further (extra-striate) visual areas of the neocortex.

Recent comparative studies have shown a positive correlation between the overall size of the neocortex and social group size (Sawaguchi 1992; Dunbar 1992; Barton 1996). This correlation is generally considered to reflect adaptive specialization for socio-cognitive information processing. A difference of opinion has arisen over precisely what aspects of socio-cognitive information processing have been selected for. Barton (1996) suggested that the primary modifications may have been to cortical areas processing visually based social information, such as facial expressions and gaze direction. Joffe & Dunbar (1997) agree that visual inputs have been modified together with changes in higher level socio-cognitive systems, but argue that, because non-V1 neocortex is more highly correlated with group size than is area V1 'visual cortex does not seem to be involved in the maintenance of social group size directly'. It is important to note, however, that non-V1 neocortex is not 'non-visual', as it contains many higher visual and polysensory processing areas, and I am able to show here that V1 and non-V1 show similar patterns of correlated evolution with the LGN, indicating that visual specialization has been a pervasive factor in neocortical evolution among primates.

2. METHODS

Data are available on the volume of V1, LGN, neocortex and the whole brain for 34 species, and on the number of neurons and volume of separate parvocellular and magnocellular LGN layers for 14 species. Non-V1 neocortex was calculated by subtracting V1 volume from total neocortex volume (Joffe & Dunbar 1997). Ecological data (activity timing, percentage frugivory and social group size) were compiled from primary

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and secondary literature. All data and sources are presented in table 1 in an electronic appendix on the Royal Society Web site at (http://www.pubs.roysoc.ac.uk/publish/pro.bs/oct98pb2.htm).

The logic underlying the comparative method is that similar regimes of selection produce similar traits in separate taxa (Harvey & Pagel 1991). Thus, in order to infer evolutionary associations among traits, it is necessary to demonstrate that they have evolved together consistently in separate lineages. Individual taxa, such as species, cannot be treated as independent in comparative analyses, because traits are shared through common inheritance as well as through independent evolution. For example, attempts to analyse the evolutionary effects of activity timing among primates must take into account the non-random taxonomic distribution of this character: of the two suborders, the strepsirhines are predominantly nocturnal while the haplorhines are predominantly diurnal. However, there have been several independent evolutionary transitions in activity timing within the primates, and these transitions provide a sample for statistical analysis. In the current data set, there are two separate lineages of diurnal lemurs and two separate lineages of nocturnal haplorhines, each lineage providing an independent comparison with its ecologically dissimilar close relatives. I use the CAIC computer package (Purvis & Rambaut 1995), which implements Felsenstein's (1985) method of independent comparisons, with modifications by Pagel (1992) and Purvis (Purvis & Rambaut 1995). The program computes contrasts in trait values between pairs of taxa at each node of the phylogeny, allowing analysis of correlated evolutionary change in those traits. The phylogeny used, including branch lengths, was taken from Purvis (1995). All continuous variables were log-transformed prior to calculating the contrasts. The resulting contrasts were then subjected to standard methods of linear bivariate and multiple regression, with all regressions forced through the origin (Purvis & Rambaut 1995).

The hypothesis that the evolution of brain size in primates is associated with visual specialization predicts that visual brain structures are disproportionately expanded in species with large brains. That is, these structures are expanded relative to the size of the rest of the brain. To generate measures of relative evolutionary change in the size of each visual structure, contrasts in structure volume (or neuron number) were regressed on contrasts in the volume of the rest of the brain, and residuals computed. These residuals are referred to as the 'relative size' (or relative neuron number) of a structure. The control variable for computing relative size, the rest of the brain, was defined as brain − (neocortex+LGN). The whole neocortex was subtracted from brain size, rather than just neocortical area V1, because much of the rest of the neocortex consists of further (extrastriate) visual areas to which the V1 projects, and these have been systematically measured in only one species (Drury *et al.* 1996). Including the non-V1 neocortex in the rest of the brain—the control variable—would therefore have had the undesired effect of partialling out the effects of cortical visual specialization—the phenomenon of interest here. Furthermore, I was interested in analysing whether V1, non-V1 and total neocortex size show similar patterns of correlated evolution with the LGN, which would indicate the pervasiveness of visual specialization in primate neocortical evolution. Encephalization (brain size relative to body size) was computed by regressing total brain volume contrasts on contrasts in body weight, and computing residuals. All residuals were based on least-squares regression, as this produces values that are strictly uncorrelated with the control variable (Harvey & Pagel 1991).

3. RESULTS

(a) *Visual specialization and encephalization*

The relative sizes of the visual structures LGN and V1 are positively correlated with encephalization (LGN; $t=2.6$, d.f.$=31$, $p=0.014$: V1; $t=2.21$, d.f.$=31$, $p=0.03$). The amount of variance explained in each case is, however, modest ($r^2=0.18$ and 0.14, respectively). Inspection of regression plots revealed one anomalously large outlier in each case, larger than the mean residual for the rest of the data by 3.9 and 4.5 standard deviations, respectively, for the V1 and LGN. The independent contrasts method is particularly sensitive to noise in the data at low taxonomic levels, sometimes warranting the exclusion of outlying contrasts (Purvis & Rambaut 1995). The outlier in this case is the contrast between the subfamilies Daubentoniidae and Indriidae, which is indeed near the tips of the phylogeny (Purvis 1995). Significantly, the phylogenetic position of *Daubentonia*, which affects the calculation of the contrast, is highly contentious (Yoder 1994). When this one contrast was removed, the fit of the linear regression was substantially improved ($r^2=0.46$ and 0.34, and $p<0.0001$ and $p=0.0005$ with d.f.$=30$, for LGN and V1, respectively).

The relative expansion of visual geniculo-cortical systems in large-brained species is reflected in a net expansion of the whole neocortex: relative neocortex size is positively correlated with encephalization ($r^2=0.33$, $t=4.32$, d.f.$=39$, $p=0.0001$). Is this net expansion a product of size differences only in the dedicated, lower-level visual areas, or is the relative size of non-V1 neocortex also associated with encephalization? Multiple regression shows that both the non-V1 and LGN are independently correlated with encephalization, but the relationship is stronger for the LGN (non-V1; $t=2.0$, $p=0.06$: LGN; $t=3.0$, $p=0.006$: $n=30$). There is a similar finding for the V1, although here the result is marginal for the V1 and stronger for the non-V1 (non-V1; $t=2.4$, $p=0.02$: V1; $t=1.9$, $p=0.07$: $n=30$). The reduced strength of the correlation for the V1 in the latter analysis does not contradict the visual specialization hypothesis, because the non-V1 contains visual areas to which the V1 projects. The two neocortical components are subdivisions of the same functional system. These data therefore do not allow us to test the hypothesis that non-visual areas are correlated with encephalization, but they certainly indicate that visual areas are.

Which of the two visual sub-systems within the geniculo-cortical system has selection acted upon to influence encephalization? The relative number of neurons in parvocellular LGN layers is positively correlated with encephalization, whereas no such relationship exists for the relative magnocellular number of neurons (figure 1). The same result is obtained when encephalization is analysed with the volume, rather than the number of neurons, of each layer (parvocellular: $t=2.47$, d.f.$=11$, $p=0.03$; magnocellular: $t=0.56$, d.f.$=11$, $p=0.59$). Hence, the visual specialization underlying encephalization is specifically parvocellular.

(b) *Visual specialization and neocortex size*

There is a strong positive correlation between relative neocortex size and the relative number of neurons in

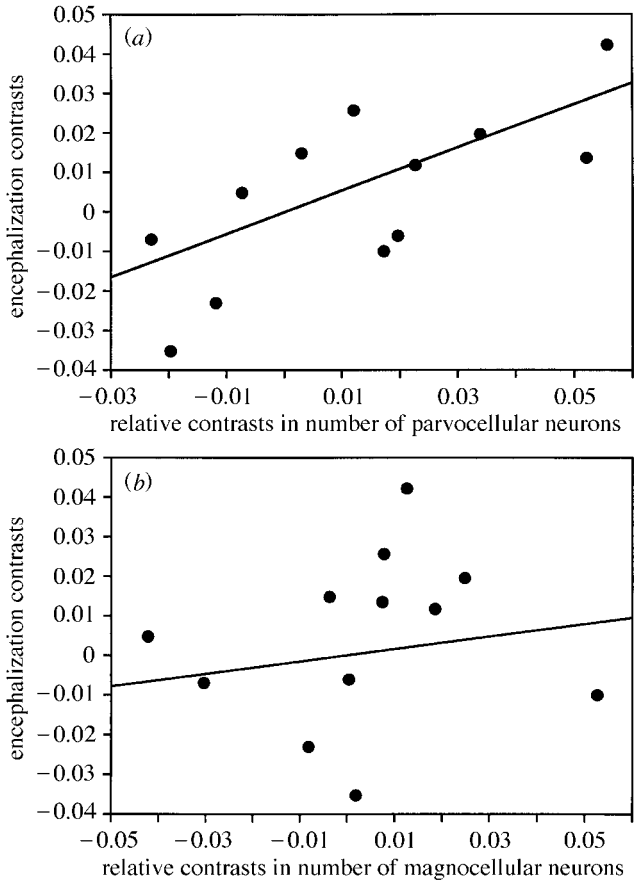

Figure 1. Correlated evolution of encephalization and the relative number of neurons in (*a*) parvocellular layers and (*b*) magnocellular layers of the LGN. Encephalization scores are the residuals from regressions of brain volume contrasts on body weight contrasts. Relative neuron number scores are the residuals from regressions of contrasts in the number of neurons on contrasts in the volume of the rest of the brain (brain volume − (neocortex+LGN)). In each case, an anomalous outlier was removed before carrying out the regression (see text). The regression is significant for parvocellular layers ($r^2=0.52$, d.f.$=11$, $p=0.005$), but not for magnocellular layers ($r^2=0.03$, d.f.$=11$, $p=0.56$).

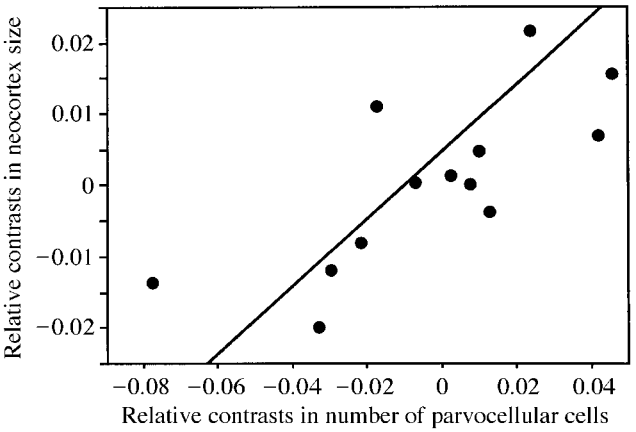

Figure 2. Correlated evolution of neocortex size and relative number of parvocellular neurons. $r^2=0.49$, $t=3.38$, d.f.$=12$, $p=0.006$. Relative contrasts are the residuals from regressions on contrasts in the size of the rest of the brain (brain − (neocortex + LGN)).

parvocellular layers of the LGN (figure 2). It is not simply the primary visual area of the neocortex that has evolved with the parvocellular LGN: this relationship is exhibited by both the V1 ($r^2=0.77$, $t=6.36$, d.f.$=11$, $p<0.0001$) and non-V1 neocortex ($r^2=0.43$, $t=2.98$, d.f.$=11$, $p=0.011$). In contrast, magnocellular layers of the LGN have not evolved with total neocortex size ($r^2=0.13$, $t=1.33$, d.f.$=11$, $p=0.21$), the size of the V1 ($r^2=0.15$, $t=1.48$, d.f.$=11$, $p=0.16$) or non-V1 neocortex ($r^2=0.09$, d.f.$=11$, $p=0.30$). Hence, as with the overall size of the brain, the relative expansion of the neocortex is associated with variance in a functionally specific part of the visual system.

(c) *Ecological correlates of visual specialization*

The relative number of parvocellular neurons is significantly greater in diurnal than in nocturnal lineages, based on four independent contrasts in activity timing ($t=16.0$, d.f.$=2$, $p=0.0005$). The same is true for relative parvocellular volume ($t=9.7$, d.f.$=2$, $p=0.002$). For the magnocellular layers, there is a small, though significant, difference in the same direction for the number of neurons ($t=3.4$, $p=0.04$), but no significant difference for volume ($t=2.2$, $p=0.1$). The general difference between nocturnal and diurnal species in the ratio of parvocellular size to magnocellular size (Hassler 1966; Shulz 1967) is therefore due to larger parvocellular layers, and not smaller magnocellular layers, in diurnal primates. Amongst the diurnal species, a stepwise multiple regression, controlling for size of the rest of the brain, shows that the number of cells in parvocellular layers is positively correlated with both percentage frugivory (partial $F=14.0$, d.f.$=3, 3$, $p<0.05$) and social group size (partial $F=20.6$; d.f.$=2.4$, $p<0.01$). The same result is obtained when the volume, rather than number of neurons, of parvocellular layers is analysed (frugivory; partial $F=10.1$, d.f.$=3, 3$, $p<0.05$: social group size; partial $F=34.3$, d.f.$=2, 4$, $p<0.01$). These ecological correlates of parvocellular LGN are identical to those previously found for neocortex size (Barton 1996). The magnocellular layers, however, show none of these correlations (all partial F values <1.0, $p>0.5$), emphasizing the evolutionary dissociation between these functionally distinct pathways. Among nocturnal species, similar analysis revealed no significant ecological correlates of either parvocellular or magnocellular variables.

4. DISCUSSION

The results suggest that large brains have evolved among primates at least partly through selection on specific types of visual mechanisms. The association between encephalization and visual specialization helps to explain why, amongst primates, frugivores have large brains for their body size (Clutton-Brock & Harvey 1980), a result that has recently been confirmed using the method of independent contrasts (Barton 1998). The most widely accepted interpretation of this correlation is that frugivores have been selected for the ability to store and integrate information on the spatio-temporal distribution of a patchy food supply (Clutton-Brock & Harvey 1980; Milton 1988). A rival hypothesis is that diet imposes a

metabolic constraint on the whole brain rather than selecting for specific information processing capacities (Martin 1981, 1996). The results reported here instead suggest an evolutionary link between encephalization and visual functions mediated by the parvocellular system, *viz* the analysis of fine detail with colour. In particular, the parvocellular, but not magnocellular, pathway is sensitive to wavelength (Livingstone & Hubel 1988; Zeki & Shipp 1988; Allman & McGuinness 1988), and V4—the cortical area specialized for colour analysis (Zeki 1993)—receives primarily parvocellular input. A number of other researchers have independently suggested that colour vision and frugivory have co-evolved in primates (Wallace 1891; Mollon 1989; Jacobs 1993, 1995). Dichromatic vision (present in diurnal lemurs and many New World monkeys) enables animals to distinguish between fruits of different colour, while trichromatic vision (present in some New World monkeys and all Old World monkeys) aids in the perception of fruits against a background of green leaves (Jacobs 1995; Osorio & Vorobyev 1996). Hence, the large brains of frugivores may be products of selection on parvocellular-mediated colour vision. Caution in over generalizing this argument should be exercised, particularly given the intraspecific variation in colour vision among New World monkey species (Jacobs 1995). Certainly, the other functions of the parvocellular pathway (Livingstone & Hubel 1988; Zeki & Shipp 1988) should also be considered. Sussman (1991), for example, suggests that the origin of primate specializations, including specializations of the visual system, may be related to the need for visually mediated fine discrimination and coordination, associated with manipulating small fruits and seeds, behaviours that would rely heavily on the acuity of parvocellular mechanisms. It may have been a combination of selection on colour vision and on other aspects of parvocellular functioning that generated brain size variation. Further comparative studies, of functionally specialized extra-striate cortical visual areas, are needed to evaluate these hypotheses.

Some authors have proposed that body size is evolutionarily more labile than brain size, so that encephalization reflects evolutionary changes in body size behind which brain size has lagged, rather than selection on brain functions (Deacon 1990). On this view, the high encephalization of frugivores reflects dietary constraints on body size, not diet-related neural specialization (Deacon 1990; Byrne 1995). To sustain this belief in the light of the results reported above, it would seem necessary to argue unparsimoniously that the correspondence between relative visual expansion and encephalization is coincidental, the former resulting from selection on brain function, the latter from selection on body size. Another problem for the brain lag explanation is that frugivory is not thought to be to be closely related to size (Fleagle 1998, pp. 234–236). There is no correlation between evolutionary changes in body weight and degree of frugivory, either within the current data set ($r^2 < 0.001$, d.f. $= 32$, $p = 0.92$), or for a larger data set of 68 primate species ($r^2 = 0.01$, d.f. $= 67$, $p = 0.37$). The same goes for the other correlate of brain size, group size ($r^2 = 0.03$, d.f. $= 67$, $p = 0.18$ for the current data set and $r^2 = 0.003$, d.f. $= 32$, $p = 0.75$). Finally, new comparative evidence does not support the assertion that brain-size lag has occurred in primates (Deaner & Nunn 1998).

The identity between the ecological correlates of parvocellular LGN size in primates—diurnality, frugivory and social group size—and those found for relative neocortex size (Barton 1996), implies that neocortical evolution is intimately associated with visual specialization. The finding that both the V1 and non-V1 neocortex have evolved together with the parvocellular layers of the LGN indicates that visual specialization has not been restricted to modifications of early visual processing mechanisms (cf. Joffe & Dunbar 1997), but includes extra-striate mechanisms too. The correlation with activity timing reflects the fact that parvocellular functions such as colour vision depend on photic conditions (daylight). The visual cues exploited by diurnal frugivores are therefore not available to nocturnal species. Instead, nocturnal frugivores may rely more on olfaction (Barton *et al*. 1995). Nocturnal owl monkeys (*Aotus nancymai*), for example, are more efficient at finding fruit using olfactory cues than are diurnal capuchin monkeys (*Cebus apella*) (Bolen & Green 1997). On the other hand, owl monkeys are functionally monochromatic (Jacobs 1995), and have only one quarter the number of parvocellular LGN neurons that capuchins have (see table 1, Appendix A on the Royal Society web site at http://www.pubs.royalsoc.ac.uk/publish/pro_bs/oct98pb2.htm)). Clearly, selection has favoured different sensory modalities according to ecological constraints. The larger size of olfactory brain structures (and perhaps also auditory structures) in nocturnal species seems to have offset the smaller size of their visual structures (Barton *et al*. 1995), so that activity timing, unlike diet and social group size, is not consistently associated with differences in overall brain size (Barton 1998).

Correlations between social group size and neocortex size have been interpreted as evidence for selection on social cognition (Sawaguchi 1992; Dunbar 1992; Barton & Dunbar 1997). Social cognition in primates depends extensively on visual processing of complex and rapid social interactions, and certain cortical areas are specialized for handling such processing (Brothers 1990). Coalition formation, for example, which is common in large social groups of anthropoid primates (Harcourt & De Waal 1992), requires the animal to integrate and interpret information about the shifting 'dispositions and intentions' (Brothers 1990) of several conspecifics simultaneously. The suggestion that the neocortical modifications associated with life in larger groups primarily involve areas specialized for visual processing of social information (Barton 1996) has received some support here. Parvocellular LGN layers, which project to the neocortex, have evolved with social group size. Magnocellular-mediated analysis of spatial relations and movement probably plays a role in processing social information, but the present results imply that the critical developments during primate evolution were enhancements of the parvocellular processing of fine details of dynamic social stimuli, known to occur in extra-striate areas such as inferotemporal cortex, and including facial expressions, gaze direction, posture, and subject–object interaction (Brothers 1990; Perrett *et al*. 1992). The capacity to hold this information in working memory while processing its emotional significance and planning responses would also

place extra demands on prefrontal cortex (Goldman-Rakic 1996).

The evolution of the primate brain is evidently linked to natural selection on specific visual mechanisms. Whilst ontogenetic constraints may impose some limit on the extent to which individual brain structures can evolve independently of one another (Finlay & Darlington 1995), there is clearly also scope for neural specialization.

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